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ratt was to be just a bit careless, to say the least, in arranging loose material, to believe implicitly that the Douglas ticket was rightly placed, against such cumulative evidence to the contrary.

Rockford, Ill.

Intracellular Pangenesis.

DR. J. W. MOLL.

This is the title of a book by Prof. Hugo de Vries, which has just appeared in the German language.¹ and will no doubt create considerable interest. The subject with which it deals is one of the highest importance, and of the manner in which it has been treated I will try to give a short account.

By many investigators of organized nature, and especially by those who have studied the phenomena of heredity, the necessity has been felt of assuming that hereditary characters in animals and plants are the visible effects produced by the nature of those substances which constitute living organisms. Hence many speculations have arisen about the structure which these substances may possess, and about the manner of their dispersion through the living body. However hopeless such attempts to penetrate into one of the greatest mysteries of nature may at first sight appear, some light certainly has been thrown on this matter through the exertions of several distinguished naturalists.

Among these Charles Darwin, without doubt, ought to be named in the very first place, and the chief object of this book is to induce in its readers a more just and higher appreciation of one of the most fertile conceptions of this illustrious author.

But others have studied the same subject, and of these the principal are Herbert Spencer, Haeckel, Nägeli, and Weismann. A comparative and critical consideration of the different views to which the above named authors have been led is the subject of the first part of Prof. de Vries's book.

In the first place, he ably shows that Darwin's so-called provisional hypothesis of pangenesis² essentially consists of two well defined and in many respects independent parts:

1. All hereditary characters of an organism are repre-

¹ Jena, Gustav Fischer, 1889.

² The Variation of Animals and Plants under Domestication. Vol. ii. p. 349.

sented by separate particles of living matter. Of these there are as many kinds as there are characters, and Darwin has called them "gemmules." Their principal attributes are that they are capable of growth and reproduce themselves, and that they can remain latent for a long time, even during many generations. In this case the hereditary characters with which they correspond do not become visible, but after a certain time they may reappear. When cell-division takes place, the gemmules are equally divided in the two nascent cells, and this is one mode of migration, by which the several organs and tissues of the body acquire their hereditary characters.

2. There is still another mode of migration, as it is assumed that every separate part of the whole organization throws off its gemmules, which are dispersed throughout the whole system, and are collected from all parts to constitute the sexual elements and buds, from which new beings are developed.

The second position was much insisted upon by Darwin, as he thought this assumption necessary to explain the hereditary effects of use and disuse, the occurrence of graft-hybrids, and the direct action of the male element on the female.

Our views upon this part of the subject have been much changed since Weismann³ has shown that those cases in which characters, seemingly acquired in later life, are transmitted to the offspring, do not necessarily prove a transmission of these characters from the altered organs to the germ which will become a new individual. They can be explained as well by assuming that the peculiar structure of the germ, from which the first varying individual sprung, caused the subsequent variations also, and that they were thus transmitted from germ to germ.

Hence there remain only a few, seldom occurring cases, which seem to be inexplicable, if migration of gemmules is not conceded. But as some of these cases can be explained otherwise, and all stand in need of further investigation, there are now no sufficient reasons to support the theory that gemmules migrate from all parts of the organism in order to unite in some other parts.

Those authors, however, who are opposed to the migration theory, have mostly thought that with it the whole hypothesis of pangenesis fell. But this, obviously, is a grave error, as the first and essential supposition of the hypothesis remains unshaken by these arguments.

³ Ueber die Vererbung, 1883.

On the single assumption that there exist "gemmules," in Darwin's sense of the word, and that these are transmitted by cell-division through all parts of the system, it still remains possible "to connect under one point of view several grand classes of facts," of which the principal are: all forms of asexual and sexual reproduction, heredity, variability, reversion, regrowth of amputated parts, and development of organisms in all its forms, whether normal or abnormal.

Darwin's pangenesis, notwithstanding its usefulness and simplicity, has been exposed to many misunderstandings, and this may partly be attributed to the great stress laid by its author upon the migration of gemmules; partly also to the fact that the term "gemmules" itself was not happily chosen. It has certainly been misinterpreted by some authors in the most unaccountable manner, and as, moreover, the idea of wandering particles is closely connected with it, de Vries does not use this term. The particles, to which the development of hereditary characters is due and which, according to his view, do not migrate through the whole organism, are called by him "pangens" (Pangene). Though this word, as well as that of pangenesis itself, will, without doubt make the hairs of a strictly grammatical reader stand on end, we will adopt it without scruple, because it is short and expressive. Moreover, its illegitimate origin will guard it against being misunderstood, as the term gemmules was.

Besides Darwin, as I have already observed, others have at one time and another tried to solve the same problem, and we will follow de Vries in his discussion of these several hypotheses.

That of Elsberg-Haeckel is especially characterized by the view that the material basis of heredity is to be sought for in the chemical molecules which constitute living protoplasm. Now it is certain that in the end the laws of heredity will be explained by the molecular phenomena of living beings. But as yet we are still very far from this point, and we are forced to assume that the particles of substance to which the appearance of hereditary characters is due, are capable of assimilating food, of growing and of reproducing themselves. There is no theory in existence which can explain from a purely chemical point of view, and merely by making use of the known properties of chemical molecules, these wonderful phenomena. Thus we are led to believe that if hereditary characters are bound to certain substances, the molecules of these substances are united into particles of

a much higher order, and approaching in their complexity of structure, power of growth, and self-division, the lowest organisms themselves. This has already been pointed out by Darwin, and if this be conceded, it obviously follows that these particles are not identical with chemical molecules in the proper sense of the word. The truth of this has perhaps in some measure been felt by Elsberg and Haeckel when they gave to the molecules, which represent hereditary characters, the distinctive name of "plastidules."

Some other authors, in particular Spencer and Weismann, have avoided this fault, but they do not assume, with Darwin, that every separate hereditary character of each organism is represented by a separate kind of living particles. They, on the contrary, suppose that the living matter from which an organism is developed consists of indivisible particles, each representing all hereditary characters of the species to which it belongs. It is certainly of much importance that de Vries has clearly pointed out the existence of this difference, as it will lead to a better understanding.

Spencer has called these particles "physiological units;" Weismann has given them the name of "ancestral plasmata" (Ahnen-plasmen), and he has applied his views to the more recent discoveries in cellular morphology. He is of opinion that the ancestral plasmata have their seat in the nucleus of the cell.

Though in many respects differing from the foregoing hypotheses, still Nägeli's "idioplasma" also represents all characters of the species.

This is a common feature of all these hypotheses, and their most important distinction from Darwin's pangenesis, as here it is assumed that every organism contains multitudes of different pangens, each representing a separate hereditary character, or as Darwin himself has expressed it: "an organic being is a microcosm—a little universe, formed of a host of self-propagating organisms, inconceivably minute and numerous as the stars in heaven."

The question, which of these opposed views is nearest to the truth, is amply discussed by the author, and almost the whole first part of the book is devoted to it.

First it is shown that the different and numerous hereditary characters which a species displays are in many respects independent of each other. To those who believe in the origin of species by means of natural selection, it is obvious

that the several characters, now constituting together a certain species, can not have appeared all at once, but were gained step by step, in many instances, without doubt, one by one.

The same characters often occur in many widely different species, *e. g.* the power of forming chlorophyll, tannin and many other substances, the peculiar habits of climbing and insectivorous plants, etc. All these are essentially the same in different plants, often belonging to separate families and orders.

It also often occurs that a single character, for instance hairiness or a certain coloring matter, is missing in a species, which otherwise exhibits in all its parts the same characters as other species of the same genus.

The differences between several species, and those between the several organs of a single animal or plant, are quite of the same order. This is conclusively shown by those cases in which secondary sexual characters or the different forms occurring in alternate generation furnished a foundation for many species, now recognized as the male, female or asexual forms of other species.

In many instances, also, simple bud-variations in plants have been developed by the art of man into new varieties of plants. And, lastly, it is generally known that the same peculiarities, for instance a red cell-sap, may be characteristic as well for certain species of a genus as for certain organs of a single individual.

Nobody will dispute the fact that many hereditary characters can be altered, or even can disappear, in some individuals, without other characters of the species in the same individual being in the least degree affected. An individual plant may have no hairs, or exhibit a changed color, all its other characters remaining the same as those of its parents; though it must be borne in mind that often little groups of characters are known to vary together. Breeders of animals and plants daily make use of such occurrences for improving their breed, and probably the scientific investigation of such cases will throw much light upon the nature of hereditary characters.

The cases of reversion, for instance that of stripes in horses and asses, show that often characters which belonged to far progenitors may suddenly reappear and combine with other characters which remain unaltered.

Another important fact is this, that hereditary characters

may be blended together in the same individual, even if they originally belonged to different species. This is most clearly shown by the occurrence of hybrids, which generally hold an intermediate place between the father and mother. But even in this case the characters retain their independence, as is clearly shown when these hybrids are fertile *inter se*. For in the subsequent generation generally some individuals wholly revert to the shape of their grandmother, others to that of their grandfather, and all intermediate gradations may be observed. In normal sexual reproduction in general the same rules prevail. All the foregoing facts, of which I am only able to give a brief summary, point to the conclusion that every character is bound to its own kind of material particles, and that these are in many respects independent of each other. On the other hand, it will be very difficult, if not impossible, to reconcile with these facts the view that in living beings all hereditary characters of the species are represented together by one and the same kind of indivisible particles. At all events this view is a wholly superfluous auxiliary hypothesis.

But there is more. When the different organs of the body are formed and developed, the characters of these organs gradually appear, and thus some parts become different from others. In pangenesis this offers no difficulty, as it is not inconceivable that some pangens are developed in one, some in another part of the body. But if the opposite assumption is made, we here meet with many obstacles. This subject has been discussed by Weismann, and he has been forced to the supposition that there are two strictly separate kinds of protoplasm, one of which he has called "germ-plasma" (Keim-plasma), the other "somatic plasma" (somatisches Plasma). The first of these consists of his "ancestral plasmata," and can reproduce the whole organism. Somatic plasma is developed from germ-plasma, when the vegetative organs of the body appear. It is less complex in structure, and contains only those characters which are needful for the parts to be formed.

In the higher orders of animals it may seem in some degree possible that two such kinds of protoplasm should exist, but every botanist will grant that in plants there is an overwhelming evidence against the supposition that the protoplasts of leaves and roots are widely different from those of spores and seeds. Many are the cases in which well-defined vegetative organs and even all cells of highly complex plants

can form the basis of a new being. The productions of gall-insects show in the same manner that in every part of a plant many hereditary characters lie hidden, which will only appear if a proper stimulant is applied. Thus the hypothesis of germ- and somatic-plasma, though it may have a logical foundation in Weismann's assumption of ancestral plasmata, is not at all supported by the facts observed in nature. And from this point of view it certainly is a great advantage that pangenesis has nothing whatever to do with such a secondary hypothesis.

Lastly, Spencer and Weismann both admit that when sexual propagation takes place, the physiological units or ancestral plasmata of father and mother are both to be found in the offspring. And this would lead to the assumption that in every organism all its ancestors from the beginning of organic life till the present day are represented. Both naturalists have felt the absurdity of such a proposition, and both are compelled to a new auxiliary hypothesis; Spencer supposing that dissimilar physiological units, when mixed together, tend to segregate, and Weismann taking for granted that each time, before a sexual union takes place, one-half of the ancestral plasmata are first removed, so that their number remains constant. This removal, according to Weismann, takes place when the second polar-globule is expelled from the ovum.

Pangenesis, again, has no need whatever of such an assumption, as no reason can be given why an excessive number of different pangens should associate.

From all these considerations it may be concluded with safety that pangenesis, combining all advantages of its sister-hypotheses, greatly excels them, so that it has no need of any auxiliary hypothesis whatever.

It is, moreover, much more simple in its application. Apparently this is not the case, as pangenesis assumes the existence of great numbers of different pangens in every being, whilst of ancestral plasmata or physiological units one kind suffices for the formation of the most complex organism. If, however, not a single being, but all organisms which the world contains are considered, the case is entirely reversed. Then it must be conceded that one is compelled to assume as many different kinds of physiological units or ancestral plasmata as there are and ever have been species in the world. In pangenesis, however, a relatively small number of different pangens will suffice to form by its numberless combina-

tions and permutations all living and extinct organized creatures.

It is a curious fact that Darwin himself has not laid much stress on the peculiarity of his gemmules as not representing each the whole organism, but only a single or a few hereditary characters. But he thought that this proposition was evident to all those who had studied the subject. He even thought, for a time, that his views were materially the same with those of Spencer, who wrote some years before him, although he afterwards saw that this was not the case.

Perhaps to this circumstance, also, it may be partly attributed that the hypothesis of pangenesis has as yet found few adherents among leading naturalists. But now this obstacle has been removed. The name of gemmules, which caused so many misunderstandings, is replaced by another. Last, but not least, Prof. de Vries has clearly shown that on no other known assumption can many important classes of facts be connected together so well as on that which forms the basis of pangenesis. I have no doubt that for this hypothesis a new era begins with the publication of this book.

In the second part of his book the author deals with the more recent discoveries in cellular morphology. He shows that the hypothesis of pangenesis, as set forth in the first part, is in perfect accordance with what has been brought to light for the most part long after Darwin had written his hypothesis. It is only natural that in applying it to the microscopical structure of cells some questions arise. These have been answered by the author, and thus some additional propositions are made, which, together with the original hypothesis, constitute what the author has called "intracellular pangenesis."

This second part of the book is much longer than the first, but it is impossible, in so short a compass as is allowed here, to mention many details, which are, however, necessary for fairly reproducing it. I must be content with giving only some faint outlines, which perhaps will induce the reader to peruse the book itself.

In the first place, it must be remembered that Prof. de Vries, in one of his former publications,⁴ has explained his views on the structure of the protoplasmic body of vegetable cells. With Hanstein, he considers the protoplasmic contents of every cell as an individual, and, with this author, he gives to it the name of "protoplast." He is opposed to

⁴ Plasmolytische Studien. Pringsh. Jahrb. xvi. p. 489.

those who consider the protoplasm as a gelatinous mass, in which here and there some bodies, such as a nucleus and plastids, are imbedded, and he calls the protoplast an elementary organism, composed of several organs, which stand in some respects in the same relation to each other as the organs of a multicellular plant. There is, however, one peculiarity in the organization of the protoplast, which is that its organs always derive their origin from similar organs. As far as is now known, they never appear in a protoplast which has not received them from its ancestors, and if a protoplast afterwards contains more organs of the same sort than it did when young, these are formed by repeated divisions. It may be said, with perfect truth, that the organization of protoplasts is a visibly hereditary one.

These views, of which I can only give a very short account, are discussed here in detail, as recent discoveries, partially made under the auspices of Prof. de Vries himself, have contributed much to confirm them. As for the nucleus, it is now generally known that this must be a very important organ, that it propagates itself by division, and never appears except where this has taken place. The same has been proved for plastids by Schmitz, Schimper and Arthur Meyer.

By Prof. de Vries himself it has been shown that vacuoles have a wall of living protoplasm, which can easily be separated from the other parts of the protoplast. He has called this wall "tonoplast," and has conclusively shown that it must be considered also as a separate organ, in all probability for producing cell-sap. Now the question remained, whence did the protoplast derive its tonoplasts and vacuoles, and this has been solved by Went, who has found that all vegetable cells, even the very youngest, contain vacuoles; that they can divide themselves or be divided, and thus multiply; and that in those cases in which formerly the appearance of vacuoles in homogeneous protoplasm was assumed, they are already present, but have been hitherto overlooked.

Another of Prof. de Vries's pupils, Wakker, has found that the so-called aleurone-grains are nothing else than the dried up albuminous contents of vacuoles in seeds, and that crystals in living cells are formed within the vacuoles.

Thus the whole protoplast appears as an organized individual, with its nucleus, plastids (which in many cases form starch), and tonoplasts (always containing cell-sap, often crystals or aleurone-grains). In the remaining part of the

protoplast a homogeneous superficial layer, which probably produces the cell-wall, can be distinguished from the inner granular mass, which is almost always in motion. It is in accordance with the author's views to see in these two parts, also, peculiar organs of the protoplast, and to suppose that the one can not be formed out of the other. He elaborately shows that, for the present, there are no facts proving such a transition, and that this subject deserves being thoroughly investigated.

At all events there is ample evidence to prove that the protoplast is an elementary organism, possessed of an hereditary organization. When cell division takes place, each daughter-cell receives its several organs as such from its parent cell, and there are no cases on record in which these organs have been independently formed from a homogeneous protoplasmic mass.

This conception of cell-division is called by the author the "panmeristic" view, in opposition to the old "neogenetic" view, which supposed that the organs of the protoplast could be newly formed after the cell is divided. As far as nucleus and plastids are concerned the neogenetic view has already been abandoned by most authors.

In the second place, the progress in our knowledge of the process of fecundation is amply discussed. It is shown that, according to the latest discoveries, it is the union of two nuclei which chiefly characterizes this process.

In the conjugation of algæ only the nuclei penetrate each other. The same is the case when a properly so-called fecundation takes place, in spermatozoa and pollen-grains the nucleus only penetrating into the ovum and uniting with its nucleus.

From these facts it appears that after fecundation in the higher organized plants the germ-cell, in truth, only contains a fecundated nucleus, whilst all other hereditary organs of its protoplast are derived only from the mother-plant.

The author applies these several facts and views to the hypothesis of pangenesis. In explaining this we will, for convenience, suppose that the pollen of one species fecundates the ovum of another allied species, and that in this manner a hybrid is formed which, as usual, in all its characters is midway between the parent plants. Common sexual reproduction is essentially the same process, and therefore the conclusions to which we come in this manner are applicable to all other cases.

As a single nucleus has sufficed for fecundation, it is clear that, on the basis of pangenesis, this must have contained pangens, representing all hereditary characters belonging to the father-plant. But all organs of the hybrid are hybridized (plastids, vacuoles, etc.), and hence it follows that the hybrid nucleus can influence in some manner all other organs of its protoplast, and thus all hereditary characters of the species.

Now the question remains, how it is possible that the nucleus exercises such an influence. Various answers can be given. Some authors maintain that a certain dynamic influence is transmitted from the nucleus to all other parts of the living protoplast; others propose the doctrine that certain enzymatic substances emanate from the nucleus and can produce changes in the surrounding protoplasm. On both these suppositions (and if it be conceded that the nucleus contains all sorts of pangens) it must be assumed that in all other organs of the protoplast there are peculiar substances, capable of growth and propagation, and producing through the dynamic or enzymatic influence from the nucleus those visible effects of which the pangens are the representatives. For, as has been shown, tonoplasts, plastids, etc., can propagate their kind, and it is through the activity of these organs of the protoplasts that hereditary characters become manifest. It is obvious that here is a secondary hypothesis of which there is no need. For if it is assumed, with Darwin, that not only the nucleus, but all other organs of the protoplast, in short living protoplasm in the widest sense of the word, consists of pangens, and of these only, the hypothesis of two kinds of self-propagating particles, corresponding with hereditary characters, becomes gratuitous. And at the same time, the supposition of a dynamic or enzymatic influence, issuing from the nucleus, can on this view be dismissed, whilst in its place comes the much simpler suggestion that pangens can migrate from the nucleus to all other organs of the same protoplast, of which it forms the center.

Our present views on the origin of species independently lead to the same conclusion, as it is clear that in the first organisms without nucleus, pangens were diffused throughout the whole protoplast, and were afterwards combined in one body when a nucleus made its appearance.

The hypothesis, explained in the foregoing lines, is called by Prof. de Vries that of "intracellular pangenesis." Giv-

ing a brief recapitulation, it can be said to consist of the following assumptions: The nucleus of every cell, used in propagation, contains all sorts of pangens of the species of animal or plant to which it belongs. As all other nuclei of the full-grown being owe their origin to repeated divisions of the first one, they all can be in possession of a complete set of pangens, which can propagate themselves when a division takes place. In the nucleus the greatest part of them remain inactive through life, with the exception only of those pangens which determine the visible characters of the nucleus itself, such as its peculiar mode of division, etc.

All other organs of the protoplast essentially contain only pangens corresponding to the characters which they are capable of displaying. It is, however, by no means necessary that they all are at all times in an active state, as, for instance, plastids in some cases are known to exhibit alternately their power of forming starch and that of forming colored matter. But, no doubt, at most times these organs contain a large amount of active pangens.

Inactive pangens from the nucleus can migrate to those other organs of the protoplast, whose characters they represent; they can again propagate themselves here, and in most cases sooner or later become active, thus bringing to light certain characters.

This migration, as shown by the facts of sexual reproduction, must occur soon after fecundation has taken place, but there is no reason why it could not happen in many other phases of development, perhaps even every time a cell-division is achieved. The author is of opinion that the migration of pangens from the nucleus to other parts of the protoplast may be effected by the movements of protoplasm, to which view there is the less objection as it has been lately shown that these movements are by no means wanting, even in the very youngest vegetable cells.

From the foregoing review it is obvious that on the assumption of intracellular pangenesis the possibility of pangens migrating from one part of the body into other parts is not at all excluded. This will be readily assented to if it is recollected that of late years many facts have been accumulated proving that the protoplasts of neighboring cells are connected together by fine protoplasmic filaments passing through the cell-walls. Moreover, Prof. de Vries himself has rendered it highly probable that the movements of pro-

toplasm are the means by which alimentary and other substances are transported through the vegetable body.

But it must be borne in mind that if the possibility of a migration of pangens from cell to cell be conceded from an anatomical point of view, this by no means suffices for the assumption that it actually does take place. And as Weismann has shown that there are no facts in heredity imperatively requiring such an explanation, a migration of pangens through the whole body is excluded from the hypothesis of intracellular pangeneses.

Moreover, in confining the migration of pangens within the limits of a single protoplast, there is only assumed that inactive pangens can leave the nucleus and sooner or later become active in other parts of the protoplast. But if the assumption of free migration through the whole body shall have any connection with the facts of heredity, a further hypothesis is necessary, viz.: that pangens, coming from all parts, are able to enter into the nuclei of those cells, which will serve for propagation. But, as has been shown, this hypothesis can be dispensed with.

It would, of course, be a delusive fancy to think that on so complex a subject as that which has been so ably treated by Prof. de Vries, the greater part of scientific men will at once, or even at a not very distant period, become of the same mind; and he himself is probably well aware that some of his propositions will be vigorously attacked. Moreover, he has chiefly treated his subject from a botanical point of view, and in a few cases, perhaps, there will be some difficulty in applying his hypothesis to the animal organism. But there is a great probability that such difficulties will not prove to be permanent ones.

At all events, even those most opposed to his views will be forced to acknowledge that intracellular pangeneses has been expounded by one who has fully mastered his subject, and that it certainly deserves to be carefully considered in all its parts, be the conclusion to which such consideration leads what it may.

It is from this conviction that I have not thought it useless to give a short account of Prof. de Vries's book to the readers of this journal.

Utrecht, Holland.